

SYNOPTIC CLASSIFICATION AND POLLEN  
MORPHOLOGY OF *VERNONIA*  
(COMPOSITAE: VERNONIEAE) IN THE OLD WORLD

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This paper is the second in a series of two papers presenting a synoptic classification and describing the pollen morphology of *Vernonia*. The first paper treated the New World taxa (Jones, 1979b). This paper considers the genus in the Old World, i.e., Africa and southeastern Asia, and should be regarded as a tentative working classification.<sup>1</sup> Its purpose is to delimit biologically meaningful groups within *Vernonia*, thereby creating smaller "natural" groupings of a manageable size for subsequent revisionary studies. Such revisionary work will eventually lead to a refinement of this classification. Without the system proposed it would be difficult, if not impossible, to examine effectively such a large and unwieldy genus. Further, since many of the taxa are rather wide ranging, studies confined to limited geographic areas would not clarify the basic problems in *Vernonia*. Hence, the preliminary treatment presented here and in the previous work represent an attempt to bring order to the chaos that currently exists in *Vernonia*.

Smith (1969) first observed differences in the pollen morphology of the Old World Section *Stengelia* and later emphasized the heterogeneous nature of the section (Smith, 1971). Keeley and Jones (1977) subsequently demonstrated the usefulness of pollen morphology in classification of the West Indian Vernonias. Cognizant of the utility of this character, the treatment of both New World (Jones, 1979b) and Old World taxa relies heavily on pollen features, although other sources of evidence were also used. Thus, while emphasizing palynology, the system presented here actually represents a synthesis of several types of systematic data, including phytochemistry (Harborne & Williams, 1977), cytotaxonomy (Jones, 1979a) and cytogenetics (Jones, 1977). These, along with classical megamorphology, have led to the taxonomic concepts outlined here.

Techniques of pollen analysis are described in the first paper

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<sup>1</sup>Mention should be made of two recent and noteworthy floristic treatments of *Vernonia* in Africa by Hilliard (1977) and Wild (1978). Although not providing a general system of classification, their keys have proved to be workable for the purpose of identification.

(Jones, 1979b) and thus will not be repeated. Species names cited are taken directly from the herbarium labels unless an obvious error was detected. Micrographs of the six types of *Vernonia* pollen grains are shown in Figure 1.

SYNOPSIS OF THE CLASSIFICATION AND POLLEN MORPHOLOGY  
OF THE OLD WORLD VERNONIAS

Taxon	Pollen Type
Subgenus <i>Orbisvestus</i>	ACEF (rarely B)
Section <i>Orbisvestus</i>	A (rarely B)
Subsection <i>Orbisvestus</i>	A (rarely B)
Subsection <i>Strobocalyx</i>	A (rarely B)
Subsection <i>Gongrothamnus</i>	A
Subsection <i>Pawekianae</i>	A
Subsection <i>Hilliardianae</i>	A
Subsection <i>Urceolatae</i>	A
Subsection <i>Turbinellae</i>	A
Subsection <i>Distephanus</i>	A
Subsection <i>Centrapalus</i>	A
Section <i>Stengelia</i>	C
Section <i>Tephrodes</i>	E
Subsection <i>Tephrodes</i>	E
Subsection <i>Lepidella</i>	E
Subsection <i>Oocephalae</i>	E
Subsection <i>Glutinosae</i>	E
Subsection <i>Bechium</i>	E
Section <i>Azureae</i>	F

**Vernonia** Schreb.

Subgenus **Orbisvestus** S. B. Jones, *subgen. nov.*

Herbae annuae perennesve, frutices vel arbores; inflorescentiae corymbosae-paniculatae vel reductae ad capitulae solitaria; capitula flosculis ca 1-40; involucria campanulata vel urceolata; pappus biserialis vel raro uniserialis; corollae purpureae, roseae, azureae, vel luteae-aurantiaceae. Chromosomatum numerus:  $n=9, 10, 18, 20, 30$ . Pollinis granum typus A, C, E, et F vel raro B. TYPE SPECIES: *Vernonia karaguensis* Oliver and Hiern.

*Geographical distribution:* Africa, Madagascar, Indian subcontinent, southeastern Asia and associated islands to Australia.

The genus *Vernonia* consists of two subgenera, i.e., subgenus *Vernonia* in the New World and subgenus *Orbisvestus* from the tropical and subtropical Old World. Subgenus *Vernonia* has a chromosome number of  $x=17$ ; whereas, subgenus *Orbisvestus* is dibasic with  $x=9, 10$  (Jones, 1979b).

The two subgenera also differ in chemical constituents. The New and Old World species of *Vernonia* can be distinguished on the basis of their sesquiterpene lactones, which are of a simpler type in New World species (Harborne & Williams, 1977). This chemical evidence supports the hypothesis that the genus *Vernonia* has two major groups: the Old World, i.e., Africa and southeastern Asia, and the New World.

Differences are also apparent in the distribution of pollen grain types (Keeley & Jones, 1979): Pollen types E and F are found only in the subgenus *Orbisvestus*; Type D only in subgenus *Vernonia*; and Type B only in subgenus *Vernonia* with the exception of a few species in the Old World. Pollen types A and C are found in both subgenera, with type A being the most common.

A few species of *Vernonia* in subsection *Orbisvestus* have yellow to orange corollas. This corolla color is not known in subgenus *Vernonia* from the New World.

### Section **Orbisvestus**

*Pollen type:* A, rarely B.

*Geographic distribution:* Old World tropics.

### Subsection **Orbisvestus**

Herbaceous perennials to semi-shrubs or shrubs, 2 dm to 5 m tall, stems leafy; heads usually numerous; corollas reddish-purple; inner pappus of bristles, outer pappus of short bristles or small scales; pollen type A, rarely B.

*Geographical distribution:* Savannas from north central to southern Africa, also in Madagascar.

*Chromosome number:*  $n = 9$  (2 species examined),  $n = 10, 20$  (1 species examined).

*Comments:* This is a large, perhaps heterogeneous series, that merits further study.

*Pollen type:* A (two species have B). Pollen grains were examined from the following specimens:

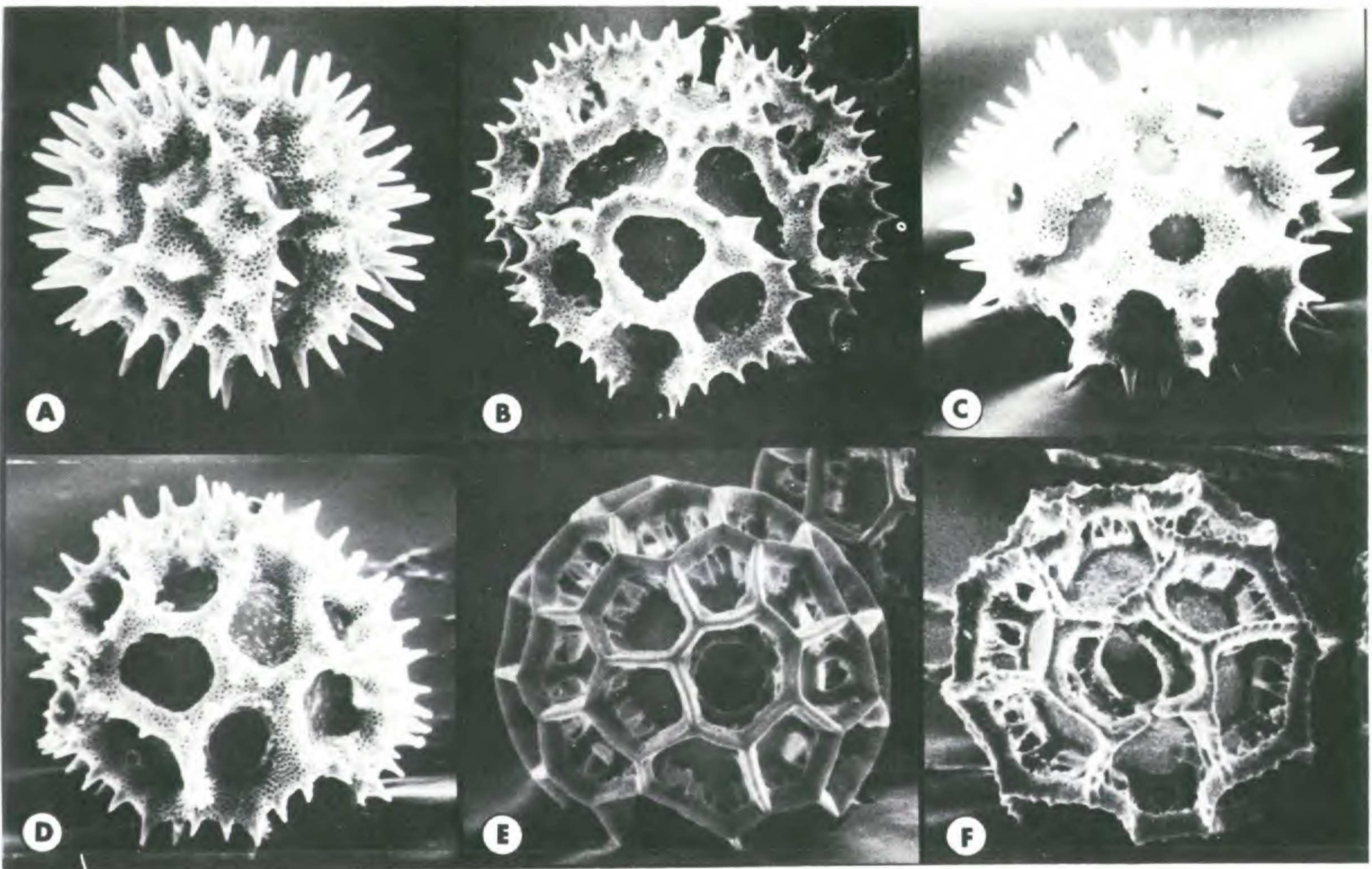


Figure 1. The six types of *Vernonia* pollen grains. **Type A:** echinate to subechinolphate, tricolporate with a continuous, micropunctate tectum, spines on the ridges or muri of the subechinolphate grains; **Type B:** echinolphate, tricolporate, with discontinuous micropunctate tectum, germinal furrows elongated, and separated at the poles by coincident muri, with spines generally pronounced on muri, but occasionally reduced, lacunae regularly or irregularly spaced, no polar lacunae present (paired poral lacunae may occur on this type as on type C); **Type C:** echinolphate, tricolporate, with a discontinuous micropunctate tectum, germinal furrows pronounced, spines on the muri or reduced in some, lacunae irregularly spaced, polar lacunae prominent, paired poral lacunae occur in some grains; **Type D:** echinolphate, triporate, with a discontinuous micropunctate tectum, spines generally pronounced on muri, occasionally reduced, lacunae regularly spaced, some of unequal size, germinal pores surrounded by a ridge; found only in the New World; **Type E:** lophate or subechinolphate, semi-tectate with elevated geometrically arranged muri, supported by conspicuous colummellae, lacunae regularly spaced, germinal pores without distinguishing features; **Type F:** echinolphate to lophate, semi-tectate with geometrically patterned elevated muri, with conspicuous colummellae, lacunae regularly spaced, germinal pores with interrupted biparted muri (types E and F are found only in the Old World).

**Vernonia amaniensis** Muschler, Tanzania: *Renvoize and Abdallah 1627* (κ). **V. antandroy** Humbert, Madagascar: *Decary 2712* (κ). **V. bamendae** C. D. Adams, Cameroun: *Keay 28410* (κ). **V. blumeoides** Hook., Nigeria: *Hepper 1642* (κ). **V. brachylaenoides** S. Moore, Zambia: *Richards 20506* (κ). **V. brachyscypha** Baker, Madagascar: *Hildebrandt 3635* (κ). **V. campanea** S. Moore, Kenya: *Drummond and Hemsley 4763* (κ). **V. cinerascens** Sch.-Bip., United Arab Republic (Egypt): *Schabetai 1409* (κ). **V. cistifolia** O. Hoffm., Malawi: *Pawek 2380* (κ). **V. cockburniana** Balf. f., Socotra I.: *Smith and Lavranos 179* (κ). **V. colorata** Drake, Tanzania: *Vesey-Fitzgerald 6795* (κ). **V. crataegifolia** Hutchins., Republic of South Africa: *Tyson 1242* (κ). **V. diversifolia** Bojer ex DC., Madagascar: *Decary 270* (κ). **V. erythromarula** Klatt, Madagascar: *Humbolt 625* (κ). **V. galpinii** Klatt, Republic of South Africa: *Hilliard 5075* (κ). **V. hildebrandtii** Vatke, Kenya: *Bally and Smith B14342* (κ). **V. holstii** O. Hoffm., Malawi: *Pawek 12734* (GA). **V. hormilantha** S. Moore, Kenya: *Jeffery 759* (κ). **V. karaguensis** Oliver & Hiern, Kenya: *Bally and Smith 14782* (κ). **V. klingii** O. Hoffm. & Muschler, Sierra Leone: *Morton and Gledhill SL 1049* (κ). **V. leopoldi** Vatke, Somalia: *Gillett 5346* (κ). **V. luembensis** DeWild. & Muschler, Zambia: *Sanane 408* (κ). **V. milanjana** S. Moore, Ethiopia: *Jackson 1943* (κ). **V. monocephala** Harv., Republic of South Africa: *Mogg 34407* (κ). **V. multiflora** DeWild., Zambia: *King 158* (κ). **V. myriocephala** A. Rich., Uganda: *Chandler 311* (κ). **V. oxyura** O. Hoffm., Malawi: *Chapman 355* (κ). **V. pectoralis** Baker, Madagascar: *Baron 3293* (κ). **V. philippsiae** S. Moore, Somalia: *Wood 1972* (κ). **V. polytricholepis** Baker, Madagascar: *Perrier 2838* (κ). **V. porphyrolepis** S. Moore, Zambia: *Richards 9503* (κ). **V. potamophila** Baker, Republic of the Congo: *Robyns 4157* (κ). **V. pteropoda** Oliver & Hiern, Kenya: *Perdue and Kibuwa 8342* (κ). **V. richardiana** Pichi-Sermolli, Ethiopia: *Gillett 14851* (κ). **V. rugosifolia** DeWild., Cameroun: *Bonghey GC10411* (κ). **V. sciaphila** S. Moore, Zambia: *Smith and Richards 4665* (κ). **V. sculptifolia** Hiern, Zambia: *Drummond and Cookson 6242* (κ). **V. sereti** DeWild., Ethiopia: *Meyer 8163* (κ). **V. stuhlmannii** O. Hoffm., Tanzania: *Welch 235* (κ). **V. turbinata** Oliver & Hiern, Kenya: *Tweedie 3328* (κ). **V. umbratica** Oberm., Republic of South Africa: *Strey 7966* (κ). **V. undulata** Oliver & Hiern, Nigeria: *Gbile and Daramola 63208* (κ). **V. unionis** Sch.-Bip. ex Walp., Ethiopia: *Pappi 77* (κ). **V. urticaefolia** A. Rich., Ethiopia: *Meyer 8175* (κ). **V. usumbarensis** O. Hoffm., Tanzania: *Faulkner 4609* (κ). **V. wollastoni** S. Moore, Kenya: *Verdcourt 1666* (κ). **V. zanzibarensis** Less., Tanzania: *Tanner 2883* (κ).

B type pollen: **Vernonia bipontiai** Vatke, Ethiopia: *Ashe 73* (GA). **V. corymbosa** Less., Republic of South Africa: *Burchell 4354* (κ).

### Subsection **Strobocalyx** (Bl. ex DC.) S. B. Jones, *stat. nov.*

Section *Strobocalyx* Bl. ex DC. *Prod.* 5: 21. 1836.

TYPE SPECIES: *Vernonia arborea* Buch.-Ham.

*Strobocalyx* (Bl. ex DC.) Sch.-Bip. *Pollichia* 18-19: 170. 1861.

*Monosis* section *Eumonosis* DC. *Prod.* 5: 77. 1836.

*Punduana* Steetz ex Peters, *Mossambique Bot. part* 6: 345. 1862-1864.

Shrubs to trees; inflorescences large paniculate, with many heads; heads from few to ca. 20 flowered; phyllaries deciduous when achenes mature; corollas whitish or pinkish to reddish-purple; outer pappus of bristles which are sometimes flattened.

*Geographical distribution:* Africa, Madagascar, and southeast Asia, usually in tropical forests.

*Chromosome number:*  $n = 9$  (1 species examined),  $n = 10$  (3 species examined).

*Comments:* This subsection is characterized by the deciduous phyllaries and the large paniculate inflorescences.

*Pollen type:* A (two species have type B). Pollen grains were examined from the following specimens:

***Vernonia ampla*** O. Hoffm., Ethiopia: *Polunin 11599* (κ). ***V. amygdalina*** Delile, Ethiopia: *Polunin 11602* (κ). ***V. antanala*** Humbert, Madagascar: *Perrier 18126* (κ). ***V. appendiculata*** Less., Madagascar: *Perrier 696* (κ). ***V. arborea*** Buch-Ham., China: *Rock 10603* (us). ***V. auriculifera*** Hiern, Ethiopia: *Mooney 5449* (κ). ***V. baroni*** Baker, Madagascar: *Bally 8335* (κ). ***V. brachycalyx*** O. Hoffm., Rwanda: *Troupin 6510* (κ). ***V. chapelieri*** Drake, Madagascar: *Humbolt 508* (κ). ***V. conferta*** Benth, Sierra Leone: *Deighton 1070* (κ). ***V. delapsa*** Baker, Madagascar: *Humbert 3843* (κ). ***V. francavillana*** Oliver & Hiern, Ethiopia: *Meyer 7677* (κ). ***V. frondosa*** Oliver & Hiern, Cameroun: *Leeuenberg 5047* (κ). ***V. glaberrima*** Welw. ex O. Hoffm., Ghana: *Hepper and Morton A3047* (κ). ***V. homollei*** Humbert, Madagascar: *Humbert 6453* (κ). ***V. livingstoniana*** Oliver & Hiern, Republic of the Congo: *Tufen 140* (κ). ***V. mespilifolia*** Less., Republic of South Africa: *Pegler 329* (κ). ***V. myriantha*** Hook. f., Cameroun: *TWM 1227* (κ). ***V. nuxioides*** O. Hoffm. & Muschler, Tanzania: *Greenway 4669* (κ). ***V. podocoma*** Sch.-Bip. ex Schweinf. & Asch., Republic of South Africa: *Thorncroft 19165* (κ). ***V. rhodopappa*** Baker, Madagascar: *Hildebrandt 3621* (κ). ***V. rubicunda*** Klatt, Madagascar: *Humbert 1088* (κ). ***V. secundifolia*** Bojer ex DC., Madagascar: *Baron 4358* (κ). ***V. subuligera*** O. Hoffm., Tanzania: *Greenway and Kanuri 11989* (κ). ***V. theophrastiifolia*** Schweinf. ex Oliver & Hiern, Ethiopia: *Meyer 7803* (κ). ***V. thomsoniana*** Oliver & Hiern ex Oliver, Cameroun: *Keay FHI 28521* (κ). ***V. titanophylla*** Brenan, Ghana: *Lock and Hall GC 43493* (κ).

B type pollen: ***Vernonia volkeriaefolia*** DC., India: Kew number *1247175* (κ). ***V. aplinii*** Hemsl., Burma: *Robertson 114* (κ).

#### Subsection **Gongrothamnus** (Steetz) S. B. Jones, *stat. nov.*

*Gongrothamnus* Steetz ex Peters, *Reise Mossamb. Bot.* 336. 1862.

TYPE SPECIES: *Gongrothamnus divaricatus* Steetz.

Erect to scandent shrubs; leaves various, usually dull green above; inflorescences compact corymbose-paniculate; corollas yellow to orange; pappus in two series, inner of bristles, outer of short flattened bristles.

*Geographical distribution:* South-central Africa, Madagascar, and southeastern Asia.

*Chromosome number:*  $n = 10$  (1 species examined).

*Comments:* The yellow to orange corollas of this group have often

caused these species to be treated as a separate genus.

*Pollen type:* A. Pollen grains were examined from the following specimens:

**Vernonia angolensis** N. E. Brown, Angola: *Gossweiler 10944* (κ). **V. auriantica** N. E. Brown, Malawi: *Pawek 11501* (GA). **V. forrestii** Anthony, China: *Rock 17347* (US). **V. garnieriana** Klatt, Madagascar: *Bernardi 11068* (κ). **V. henryi** Dunn, China: *Forrest 21069* (US). **V. lutea** N. E. Brown, South-West Africa: *Leistner 5909* (κ). **V. sublutea** Ell., Madagascar: *Mabberley 956* (κ). **V. vitellina** N. E. Brown, Republic of South Africa: *Codd 6076* (κ).

Subsection **Pawekianae** S. B. Jones, *subsect. nov.*

Frutices ramosissimae ad scandentes vel herbae perennes; folia basibus cordatis, truncatis vel late cuneatis rotundatisve; inflorescentiae corymbosae-paniculatae. TYPE SPECIES: *Vernonia angulifolia* DC. Named in honor of Mrs. Jean Pawek, prodigious collector of Vernoniae and other taxa in Malawi.

Scandent, much branched shrubs or perennials; leaves with cordate, truncate, or rounded to cuneate bases; inflorescences corymbose-paniculate; heads relatively small, phyllaries acute-acuminate to rounded-cuspidate.

*Geographical distribution:* Southern Africa.

*Chromosome number:*  $n = 9$  (1 species examined).

*Comments:* A distinctive group of largely scandent perennials, generally having broad leaves and distinct leaf bases.

*Pollen type:* A. Pollen grains were examined from the following specimens:

**Vernonia andohii** C. D. Adams, Ghana: *Fishlock 20* (κ). **V. angulifolia** DC., Republic of South Africa: *Strey 10971* (κ). **V. anisochaetoides** Sond., Republic of South Africa: *Hanagan 269* (κ). **V. biafrae** Oliver & Hiern, Liberia: *Amshoff 2430* (κ). **V. malacophyta** Baker, Madagascar: *Perrier 19865* (κ). **V. syringifolia** O. Hoffm., Malawi: *Pawek 5729* (κ). **V. tufnellae** S. Moore, Uganda: *Purseglove 580* (κ).

Subsection **Hilliardianae** S. B. Jones, *subsect. nov.*

Plantae herbae perennes, parvae; folia albida pilosa; inflorescentiae corymbosae-paniculatae vel diminutae; capitula parva, 8–15 flosculis; phyllaria lanceolata. TYPE SPECIES: *Vernonia oligocephala* (DC.) Sch.-Bip. The name honors Dr. O. M. Hilliard, student of the Compositae of Natal (Hilliard, 1977).

Small herbaceous perennials; foliage and stems whitish pilose; inflorescences corymbose-paniculate or reduced; heads small, few flowered; phyllaries lanceolate; outer pappus small, flattened scale-like bristles; achenes usually pubescent.



*Geographical distribution:* Grassland species of tropical and southeastern Africa.

*Chromosome number:*  $n = 9$  (1 species examined).

*Comments:* This is a rather natural group of grassland species. The plants, however, are variable in leaf size and shape and the number of species is probably inflated.

*Pollen type:* A. Pollen grains were examined from the following specimens:

***Vernonia calyculata*** S. Moore, Tanzania: *Geilinger 2795* (κ). ***V. dregeana*** Sch.-Bip. ex Walp., Republic of South Africa: *Werdermann and Oberdieck 1204* (κ). ***V. hirsuta*** Sch.-Bip. ex Walp., Republic of South Africa: *Hilliard 5602* (GA). ***V. natalensis*** Sch.-Bip. ex Walp., Ethiopia: *Mooney 5250* (κ). ***V. oligocephala*** (DC.) Sch.-Bip. ex Walp., Malawi: *Robson 223* (κ). ***V. pinifolia*** Less., Republic of South Africa: *Long 34* (κ). ***V. smithiana*** Less., Cameroun: *Amshoff 2535* (κ).

Subsection ***Urceolatae*** S. B. Jones, *subsect. nov.*

Frutices ad 1–4 m altis; inflorescentiae corymbosae-paniculatae; involucria urceolata, phyllariis arcte imbricatis. TYPE SPECIES: *Vernonia sphaerocalyx* O. Hoffm.

Shrubs, 1–4 m tall; stems tomentose when young; leaves elliptic to lanceolate, tomentose beneath; inflorescences corymbose-paniculate; involucria urceolate, phyllaries tightly appressed; outer pappus of short, flattened scale-like bristles; achenes glabrate to glandular or rarely sparsely pubescent.

*Geographical distribution:* South-central Africa.

*Chromosome number:* none reported.

*Comments:* A well marked group of shrubs characterized by urceolate involucria.

*Pollen type:* A. Pollen grains were examined from the following specimens:

***Vernonia elisabethvilleana*** DeWild., Republic of the Congo: *Ritschard 1609* (κ). ***V. exsertiflora*** Baker, Republic of the Congo: *Lisowski 373* (κ). ***V. fraterna*** N. E. Brown, Zambia: *Richards 5114* (κ). ***V. goetzeana*** O. Hoffm., Tanzania: *Polhill and Paulo 1692* (κ). ***V. sphaerocalyx*** O. Hoffm., Tanzania: *Eggeling 6502* (κ).

Subsection ***Turbinellae*** S. B. Jones, *subsect. nov.*

Herbae perennes; inflorescentiae corymbosae-paniculatae; involucria campanulata, phyllariis tomentosis; pappi setae 2-seriales complanatae; achenia pilosa. TYPE SPECIES: *Vernonia lampropappa* O. Hoffm.

Herbaceous perennials; stems tomentose becoming glabrate with age; leaves ovate to elliptic, tomentose, reticulate-veined beneath;

inflorescences corymbose-paniculate; involucre campanulate, phyllaries tomentose; pappus bristles in 2 series, flattened; achenes pilose.

*Geographical distribution:* South-central Africa.

*Chromosome number:* none reported.

*Comments:* a group characterized by tomentose phyllaries and flattened pappus bristles.

*Pollen type:* A. Pollen grains were examined from the following specimens:

**Vernonia eremanthifolia** O. Hoffm., Angola: *Faulkner 481* (κ). **V. lampropappa** O. Hoffm., Burundi: *Van der Ben 1999* (κ). **V. trusurilla** S. Moore, Zambia: *Richards 24450* (κ). **V. turbinella** S. Moore, Zambia: *Sanane 467* (GA).

#### Subsection **Distephanus** (Cass.) S. B. Jones, *stat. nov.*

*Section Distephanus* (Cass.) Benth. & Hook. 2:228. 1873.

*Distephanus* Cass., Bull. Soc. Philom. 1817:151. 1817. TYPE SPECIES: *D. populifolius* (Lam.) Cass. = *V. populifolia* (Lam.) Spreng.

Shrubs, often scandent, or small trees, rarely somewhat herbaceous; leaf blades variable but usually elliptic to ovate; inflorescences terminal paniculate-corymbose or axillary paniculate-corymbose; corollas usually glandular, lobes sometimes hairy; pappus of bristles 2-seriate, sometimes slightly flattened.

*Geographical distribution:* Indian sub-continent, southeastern Asia, islands of Indian Ocean, Philippines, and Australia.

*Chromosome number:*  $n = 20$  (1 species examined).

*Comments:* This is not a distinctive group of Vernonias. It is classified largely on the basis of geography and pollen type. Further study may result in redefinition of the subsection.

*Pollen type:* A. Pollen grains were examined from the following specimens:

*Vernonia anceps* Clarke, Ceylon: *Grierson 1056* (US). **V. andersonii** Clarke, Vietnam: *Petelot 2080* (US). **V. blanda** DC., India: *Parry 585* (κ). **V. celebica** (Bl.) DC., Philippines: *Ramos 1915* (κ). **V. cuneata** Less., Australia: *Brass 19291* (κ). **V. cylindriceps** Clarke, Thailand: *Garnett 629* (κ). **V. elaeagnifolia** DC., Thailand: *Zimmermann 101* (US). **V. extensa** DC., China: *Rock 7909* (US). **V. floescens** Elmer, Philippines: *Elmer 17998* (κ). **V. lancifolia** Merr., Philippines: *Vanoverbergh 689* (κ). **V. papillosa** Franch., China: *Henry 9502* (κ). **V. populifolia** (Lam.) Spreng., Mauritius Islands: *Ayres 1848* (κ). **V. salvifolia** Wight, India: *Wight 1522* (κ). **V. solanifolia** Benth., Vietnam: *Petelot 2350* (US). **V. sylvatica** Dunn, China: *Henry 11051* (κ). **V. wallichii** Ridley, Malaysia: *Sinclair 40742* (κ). **V. wightiana** Arn., Ceylon: *Moldenke 28299* (US). **V. zeylanica** (L.) Less., Ceylon: *Fosberg 50322* (US).

Subsection **Centrapalus** (Cass.) S. B. Jones *stat. nov.*

*Centrapalus* Cass., Dict. Sci. Nat. 7: 382. 1817. TYPE SPECIES: *Centrapalus galamensis* Cass.

*Xipholepis* Steetz ex Peters, Mossambique Bot. part 6: 344. 1862-1864. *Xipholepis silhetensis* Steetz ex Peters.

Section *Xipholepis* (Steetz) Benth. & Hook., Gen. Pl. 2: 229. 1873.

Coarse annuals to perennial herbs or semishrubs; leaves variable; inflorescences of single terminal heads to branched corymbose-paniculate clusters; heads relatively large; phyllaries variable; corollas blue to purple; achenes with brownish pubescence.

*Geographical distribution:* Grasslands and successional habitats south of the Sahara into South Africa.

*Chromosome number:*  $n = 9$  (2 species examined).

*Comments:* This is a well marked group distinguished by achenes with brownish pubescence.

*Pollentype:* A. Pollen grains were examined from the following specimens:

**Vernonia africana** Druce, Republic of South Africa: *Saunders s.n.* (κ). **V. fromontana** R. E. Fries, Kenya: *USDA PI 321654* (GA). **V. catumbensis** Hiern, Zambia: *Milne-Redhead 594* (κ). **V. denudata** Hutchins. & B. L. Burtt, Tanzania: *Richards 7031* (κ). **V. duemmeri** S. Moore, Uganda: *Chandler 1877* (κ). **V. fastigiata** Oliver & Hiern, Mozambique: *Pedrogas 259* (κ). **V. gerrardi** Harv., Republic of South Africa: *Hilliard and Burtt 7493* (κ). **V. inulaefolia** Steud., *Andrews A1963* (κ). **V. kamerunensis** Mattf., Cameroun: *Coboner 9421* (κ). **V. kirkii** Oliver & Hiern, Zambia: *Mutumushi 2169* (κ). **V. lukamaensis** DeWild., Republic of Congo: *Quarre 261* (κ). **V. pauciflora** (Willd.) Less., Tanzania: *Batty 1084* (GA). **V. praemorsa** Muschler, Tanzania: *Richards 15808* (κ). **V. purpurea** Sch.-Bip. ex Walp., Tanzania: *Richards 27066* (GA). **V. quartiniana** A. Rich., Ethiopia: *Fries et al. 436* (κ). **V. schweinfurthii** Oliver & Hiern, Rwanda: *Troupin 4112* (κ). **V. sutherlandi** Harv., Republic of South Africa: *Hutchinson 2248* (κ). **V. temnolepis** O. Hoffm., Angola: *Henriques 1030* (κ). **V. wakefieldii** Oliver, Kenya: *Greenway and Kanuri 12706* (κ). **V. zambesiaca** S. Moore, Zambia: *van Rensburg 2920* (κ).

Section **Stengelia** (Sch.-Bip. ex Walp.) Benth. & Hook. Gen. Pl. 2: 227. 1873.

Subsection *Stengelia* Sch.-Bip. ex Walp. Repert. Bot. Syst. 2: Suppl. 1, 946. 1843.

TYPE SPECIES: *Vernonia adoensis* Sch.-Bip. ex Walp. [See Smith (1971) for a history of section *Stengelia*.]

Herbaceous perennials to shrubs; leaves alternate or forming a basal rosette; heads borne single and terminal, or in reduced clusters, or in paniculate to corymbose inflorescences; phyllaries various, green or sometimes white to purple; corollas with relatively long

tubes, whitish to purplish; inner pappus generally long, slightly flattened or filiform, outer pappus usually short and scale-like.

*Geographical distribution:* Continental Africa south of the Sahara Desert to Natal, South Africa and in the Indian subcontinent.

*Chromosome number:*  $n = 10$  (9 species examined).

*Comments:* This is a distinctive and well marked Old World group.

*Pollen type:* C. This is the only group in the Old World with C type pollen. Pollen grains were examined from the following specimens:

**Vernonia abyssinica** Sch.-Bip. ex Hochst., Ethiopia: *USDA PI 320083* (GA). **V. acrocephala** Klatt, Cameroun: *Baver 23* (κ). **V. adoensis** Sch.-Bip. ex Walp., Zambia: *Sanane 755* (GA). **V. albicans** DC., India: *Ramamoorthy 1951* (US). **V. anthelmintica** (L.) Willd., India: *Mooney 4183* (κ). **V. bracteosa** O. Hoffm., Tanzania: *Renvoize and Abdallah 1926* (κ). **V. chthonocephala** O. Hoffm., Nigeria: *Hepper 1775* (κ). **V. filigera** Oliver & Hiern, Ethiopia: *Schimper 1530* (κ). **V. filipendula** Hiern, Zambia: *USDA PI 321669* (GA). **V. guineensis** Benth., Cameroun: *Daramola 40609* (κ). **V. hymenolepsis** A. Rich., Ethiopia: *USDA PI 320091* (GA). **V. lancibracteata** S. Moore, Rhodesia: *Ashby 20165* (κ). **V. lasiopus** O. Hoffm., Sudan: *Sillitoe 196* (κ). **V. nimbaensis** C. D. Adams, Sierra Leone: *Gledhill 359* (κ). **V. praecox** Welw. ex O. Hoffm., Republic of the Congo: *Quarre 2533* (κ). **V. procera** O. Hoffm., Nigeria: *Lely P 179* (κ). **V. pumila** Kotschy & Peyr., Uganda: *Purseglove P 1256* (κ). **V. quangensis** O. Hoffm., Angola: *Gossweiler 9526* (κ). **V. rigidifolia** Hiern, Zambia: *Milne-Redhead 3086* (κ). **V. schimperi** DC., Arabia: *Botta 1838* (US). **V. schirensis** Oliver & Hiern, Republic of South Africa: *USDA PI 32-2705* (GA). **V. stenolepis** Oliver, Tanzania: *Pielou 168* (κ). **V. subaphylla** Baker, Zambia: *Milne-Redhead 3414* (κ). **V. subsessilis** DC., Union of Burma: *Rock 7839* (US). **V. vallicola** S. Moore, Botswana: *Winter and Marais 4745* (κ).

Section **Tephrodes** DC. Prodr. 5:24. 1833. TYPE SPECIES: *Vernonia cinerea* (L.) Less.

Annual or perennial herbs, native to Africa, southeastern Asia and associated archipelagos, with type E pollen grains.

Subsection **Tephrodes**. TYPE SPECIES: *Vernonia cinerea* (L.) Less.

Annual or perennial herbs; leaves variable; inflorescences variable, corymbose-paniculate to greatly reduced and with only a few heads; involucre campanulate; phyllaries imbricate; pappus biseriate, inner pappus of bristles, outer pappus of very small scales, bristles, or scale-like bristles; achenes variable.

*Geographical distribution:* Africa, southeastern Asia and associated archipelagos.

*Chromosome number:*  $n = 9$  (9 species examined),  $n = 18$  (2 species examined).

*Comments:* This rather large group of annual and perennial species may be heterogeneous; however, additional data, i.e., chemistry, chromosome numbers, etc., are needed prior to further classification. At best, this is a tentative grouping.

*Pollen type:* E. Pollen grains were examined from the following specimens:

***Vernonia adenocephala*** S. Moore, Zambia: *Mutimushi* 3373 (κ) ***V. amoena*** S. Moore, Tanzania: *Polhill and Paulo* 2244 (κ). ***V. amplexicaulis*** Baker, Ethiopia: *Burger* 908 (κ). ***V. aschersonii*** Sch.-Bip., Somalia: *Aule* 65 (κ). ***V. atriplicifolia*** Spach, Muscat & Oman: *Fiennes B 11* (κ). ***V. attenuata*** DC., Thailand: *Hansen and Smithinard* 12722 (κ). ***V. bainesii*** Oliver & Hiern, Rhodesia: *Hanofan* 3046 (κ). ***V. bracteata*** Wall., China: *Henry* 12498 (κ). ***V. buchanani*** Baker, Zambia: *Fanshawe* 287 (κ). ***V. camporum*** A. Cheval., Ghana: *Morton* 25136 (κ). ***V. chinensis*** (Lam.) Less., Philippines: *Williams* 352 (κ). ***V. chloropappa*** Baker, Malawi: *Pawek* 11494 (GA). ***V. cinerea*** Less., Ghana: *USDA PI 318818* (GA). ***V. cistifolia*** O. Hoffm., Republic of the Congo: *Ghesquiere* 4267 (κ). ***V. congolensis*** DeWild. & Muschler, Burundi: *Lewalle* 5406 (κ). ***V. cryptocephala*** Baker, Somalia: *Newbould* 786 (κ). ***V. curtisii*** Craib & Hutchins., Malaysia: *Corner* 37834 (κ). ***V. dalzelliana*** J. R. Drumm & Hutchins., India: *Browne* 6249 (κ). ***V. daphnifolia*** O. Hoffm., Republic of the Congo: *Robyns* 4385 (κ). ***V. divergens*** Edgew., India: *Saldanha* 12223 (US). ***V. elmerii*** Merr., Philippines: *Merrill* 793 (κ). ***V. erigeroides*** DC., Timor Islands: *Kew number* 1247175-252 (κ). ***V. fysoni*** Calder, India: *Bourne* 1831 (κ). ***V. hindei*** S. Moore, Kenya: *Bally and Smith* 14755 (κ). ***V. hoffmanniana*** Hutchins. & Dalziel, Tanzania: *Milne-Redhead and Taylor* 9828 (κ). ***V. hookeriana*** Arn., Ceylon: *Grierson* 1015 (US). ***V. indica*** Clarke, India: *Saldanha* 15785 (κ). ***V. jugalis*** Oliver & Hiern, Ethiopia: *Burger* 3175 (κ). ***V. junghuhniana*** Koster, India: *Backer* 20237 (κ). ***V. kandtii*** Muschler, Tanzania: *Tanner* 5565 (κ). ***V. kenteocephala*** Baker, Madagascar: *Perrier* 12146 (κ). ***V. kerrii*** Craib., Thailand: *Srensen, Larsen & Hansen* 1602 (κ). ***V. kingii*** Clarke, Thailand: *Hansen, Seidenfaden, & Smitinand* 10862 (κ). ***V. kivuensis*** Humbert & Staner, Burundi: *Lewalle* 124 (κ). ***V. lanceolata*** Mattf., New Guinea: *Brass* 23756 (κ). ***V. loloana*** Dunn, China: *Henry* 12375 (κ). ***V. mecistophylla*** Baker, Madagascar: *Perrier* 3127 (κ). ***V. moluecensis*** (Bl.) Miq., Timor Islands: *Tsm* 8780 (κ). ***V. nestor*** S. Moore, Malawi: *Pawek* 11739 (GA). ***V. nyassae*** Oliver, Tanzania: *Richards* 7874 (κ). ***V. obionifolia*** O. Hoffm., South West Africa: *Giess* 3449 (κ). ***V. ornata*** W. A. Talbot, India: *Ambo* 7044 (κ). ***V. pandurata*** Hort. Vindob. ex Link, Republic of the Congo: *Devred* 149 (κ). ***V. patula*** (Ait.) Merr., Hong Kong: *Taam* 1830 (US). ***V. pectiniformis*** Wight, India: *Rodin* 8133 (κ). ***V. peninsularis*** Clarke, India: *Wight* 1529 (κ). ***V. perrottetii*** Sch.-Bip. ex Walp., Cameroun: *Hepper* 3991 (κ). ***V. philipsoniana*** Lawalree, Tanzania: *Harwood* 34 (κ). ***V. plumbaginifolia*** Fenzl, Nigeria: *Meikle* 1343 (κ). ***V. polysphaera*** Baker, Malawi: *Pawek* 5256 (κ). ***V. revoluta*** Hein., India: *Royle* 233 (κ). ***V. rogersii*** S. Moore, Mozambique: *Faulkner* 298 (κ). ***V. rosburghii*** Less., India: *Royle sn.* (κ). ***V. saligna*** DC., India: *Wenger* 304 (κ). ***V. scariosa*** Arn., Ceylon: *Grierson* 1060 (US). ***V. sculptifolia*** Hiern, Zambia: *Lanarl* 124 (κ). ***V. setigera*** Arn., Ceylon: *Moldenke* 28289 (US). ***V. smaragdopappa*** S. Moore, Congo: *Lisowski* 361 (κ). ***V. somalensis*** Franch., Somalia: *Bally B* 10999 (κ). ***V. squarrosa*** Less., Thailand: *Sahol* 662 (US). ***V. steetziana*** Oliver & Hiern, Zambia: *Wilberforce* 176 (κ). ***V. sutepensis*** Kerr, Thailand: *Larsen* 8794 (κ). ***V. teres*** Clarke, Nepal: *Banerjee* 3039 (US). ***V. uncinata*** Oliver & Hiern, Somalia: *Glover and Gilliland* 412 (κ).

Oliver & Hiern, Zambia: *Wilberforce* 176 (κ). *V. sutepensis* Kerr, Thailand: *Larsen* 8794 (κ). *V. teres* Clarke, Nepal: *Banerjee* 3039 (US). *V. uncinata* Oliver & Hiern, Somalia: *Glover and Gilliland* 412 (κ).

Subsection **Lepidella** (Oliver & Hiern) S. B. Jones. *stat. nov.*

Section *Lepidella* Oliver & Hiern, Fl. Trop. Afr. 3: 267. 1877.

TYPE SPECIES: *Vernonia petersii* Oliver & Hiern.

Annual or perennial herbs, 1 to 9 cm in height; pappus biseriate, inner of bristles, outer of relatively large scales; achenes 5-angled or ribbed, papillose between the ribs.

*Geographical distribution:* South-central Africa.

*Chromosome number:*  $n = 10$  (2 species examined) and  $n = 9$  (1 species examined).

*Comments:* The outer pappus and 5-angled, papillose achenes serve as distinctive features of this subsection.

*Pollen type:* E. Pollen grains were examined from the following specimens:

*Vernonia aemulans* Vatke, Malawi: *Pawek* 12735 (GA). *V. ambigua* Kotschy & Peyr., Cameroun: *Hepper* 3938 (κ). *V. centauroides* Klatt, Republic of South Africa: *Garcia* 11927 (κ). *V. fontinalis* S. Moore, Buruni Territory: *Lewalle* 5359 (κ). *V. ianthina* Muschler, Republic of the Congo: *Witte* 582 (κ). *V. jelfiae* S. Moore, Zambia: *Sanane* 822 (κ). *V. karongensis* Baker, Tanzania: *Thulin and Mhoro* 857 (κ). *V. petersii* Oliver & Hiern, Zambia: *Sanane* 1265 (GA). *V. ugandensis* S. Moore, Uganda: *Maitland* s.n. (κ). *V. viatorum* S. Moore, Zambia: *Robinson* 3775 (κ). *V. violacea* Oliver & Hiern, Tanzania: *Richards* 8448 (κ). *V. violaceo-papposa* DeWild., Zambia: *Richards* 4388 (κ).

Subsection **Oocephalae** S. B. Jones, *subsect. nov.*

Herbae perennes, rhizomate accrescenti; folia linearia vel linearia-oblonga; inflorescentiae corymbosae-paniculatae; involucria urceolata, phyllariis tomentosis; pollinis grana typus E. TYPE SPECIES: *Vernonia oocephala* Baker.

Perennial herbs from an enlarged rootstock, 0.7–1.2 m tall; leaves linear, or linear-oblong; inflorescences corymbose-paniculate; involucria urceolata, phyllaries tightly appressed, densely tomentose to only slightly tomentose; corollas creamy to reddish-purple; inner pappus of slightly plumose bristles, outer pappus of scale-like bristles to small scales.

*Geographical distribution:* South-central Africa.

*Chromosome number:* none reported.

*Comments:* A distinctive group. The species appear to need revision.

*Pollen type:* E. Pollen grains were examined from the following specimens:

***Vernonia luteo-albida*** DeWild., Zambia: *Hutchinson and Gillett 3611* (κ). ***V. oocephala*** Baker, Nigeria: *Jackson 309* (κ). ***V. stachelinoides*** Mart. ex Baker, Republic of South Africa: *Codd 2874* (κ). ***V. stenocephala*** Oliver, Zambia: *Richards 21417* (κ).

Subsection **Glutinosae** S. B. Jones, *subsect. nov.*

Frutices; folia palmatim nervata; inflorescentiae reductae; corollae luteae, lobis pubescentibus. TYPE SPECIES; *Vernonia glutinosa* DC.

Shrubs; leaves palmately veined with 3–5 main veins, elliptic-lanceolate to orbicular, tomentose to glandular beneath; inflorescences reduced and compact; involucre broadly campanulate, phyllaries densely to lightly tomentose; corollas yellow, lobes pubescent; pappus straw-colored, of uni- or biseriate bristles; achenes pubescent.

*Geographical distribution:* Madagascar.

*Chromosome number:* none reported.

*Comments:* A distinctive and well marked group.

*Pollen type:* E. Pollen grains were examined from the following specimens:

***Vernonia glutinosa*** DC., Madagascar: *Humbert 12255* (κ). ***V. ochroleuca*** Baker, Madagascar: *Haine 13* (κ). ***V. poissonii*** Humbert, Madagascar: *Mabberley 882* (κ). ***V. trinervis*** Drake, Madagascar: *Schlieben 8174* (κ).

Subsection **Bechium** (DC.) S. B. Jones, *stat. nov.*

*Bechium* DC., Prodr. 5: 70. 1836 TYPE SPECIES: *B. capiforme* DC.

Herbaceous annual or perennial; stems with reddish, capitate trichomes; inflorescences corymbose-paniculate or reduced; branches with capitate trichomes; phyllaries in 2–3 series, with capitate trichomes.

*Geographical distribution:* Madagascar.

*Chromosome number:* none reported.

*Comments:* This is the only group of *Vernonias* with stalked, capitate trichomes. It is tempting to treat this group at the generic level; however, “one character taxonomy” would not serve its best interest.

*Pollen type:* E. Pollen grains were examined from the following specimens:

***Vernonia bojeri*** Less., Madagascar: *Perrier 3255* (κ). ***V. nudicaulis*** Less., Madagascar: *Hildebrandt 3843* (κ). ***V. praetensis*** Klatt, Madagascar: *Mabberley 894* (κ). ***V. rhodolepis*** Baker, Madagascar: *Hildebrandt 3551* (κ).

Section **Azureae** S. B. Jones, *sect. nov.*

Herbae perennes, accrescentes e caudicibus crassis lignosis; corollae azureae; pollinis grana typus F. Type species: *Vernonia glabra* Vatke.

Perennial herbs, from stout woody root-stocks, 2 dm to 2 m tall; leaves variable but generally linear-lanceolate to oblanceolate; inflorescences corymbose-paniculate to solitary and terminal; heads relatively large; phyllaries linear-lanceolate, loosely imbricated in several series, tips long acuminate; corollas blue; pappus bristles variable, bi-seriate, sometimes slightly plumose.

*Geographical distribution:* South-central Africa.

*Chromosome number:*  $n = 10, 20, 30$  (3 species examined) 1 of these species has cytotypes of  $n = 10, 20,$  or  $30$ ).

*Comments:* A group of perennial herbs characterized by their enlarged woody root-stocks, blue flowers, and unique pollen grain type.

*Pollen type:* F.

Pollen grains were examined from the following specimens:

**Vernonia djalensis** A. Cheval., Guinea: *Jacques-Felix* 7065 (κ). **V. gerberaeformis** Oliver & Hiern, Tanzania: *Richards* 26235 (κ). **V. gardneri** Thw., Ceylon: *Alston* 1667 (κ). **V. glabra** Vatke, Rhodesia: *Pope* 1359 (GA). **V. hockii** DeWild. & Muschler, Zambia: *Brenan and Greenway* 7921 (κ). **V. infundibularis** Oliver & Hiern, Uganda: *Hoaws* 736 (κ). **V. melleri** Oliver & Hiern, Zambia: *Sanane* 1147 (GA). **V. Migeodi** S. Moore, Cameroun: *Letouzey* 6648 (κ). **V. obconica** Oliver & Hiern, Zambia: *Mutimushi JMM* 3763 (κ). **V. parishii** Hook. f., Thailand: *Hosseus* 458 (κ). **V. pogosperma** Klatt, Uganda: *Purseglove P* 2094 (κ). **V. rosenii** R. E. Fries, Zambia: *Kornas* 86 (κ). **V. subplumosa** O. Hoffm., Zambia: *Mutimushi* 3315 (κ). **V. superba** O. Hoffm., Zambia: *Sanane* 406 (GA). **V. usafuensis** O. Hoffm., Tanzania: *Brenan and Greenway* 8206 (κ).

#### ACKNOWLEDGMENTS

I am grateful to the herbaria cited herein for making the materials available for study. The technical assistance of the following undergraduates is acknowledged: Mr. John Tanner, Mr. Bob Grese, Mr. Rick Gardini, Ms. Marcia Stefani, Mr. Oliver Ware, and Mr. Greg Jones. Mrs. Nancy C. Coile handled the loans and assisted with editing and proof-reading the manuscript. My sincere thanks and appreciation go to Mr. Charles Jeffery for his helpful suggestions during my stay at Kew. I also wish to thank Mrs. Jean Pawek, Dr. O. M. Hilliard, Prof. H. Wild, and Mr. G. V. Pope for supplying plant material. The SEM was done at the University of Georgia Electron



Microscopy Laboratory. The National Science Foundation supported the study by several research grants.

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